

PEDICULARIS AURANTIACA AND *PEDICULARIS DENSIFLORA*
(OROBANCHACEAE): TAXONOMY, PHENOLOGY AND
FLORAL MORPHOLOGICAL VARIATION

ANNA K. MONFILS

Department of Biology, Central Michigan University, Mt Pleasant, MI 48859
monfilak@cmich.edu

L. ALAN PRATHER

Herbarium, Department of Plant Biology, Michigan State University,
East Lansing, MI 48824

ABSTRACT

We investigated patterns of infraspecific variation among populations of *Pedicularis densiflora*, including populations formerly recognized as *P. densiflora* subsp. *aurantiaca*. Several statistical analyses (UPGMA, ANOVA, and PCA) were conducted on floral traits measured in the field. All three statistical analyses indicated consistent differences in floral morphology among populations. These differences were confirmed by a review of over 1000 herbarium specimens. Two series of populations were separated, and two species recognized, *Pedicularis aurantiaca* and *P. densiflora*. *Pedicularis aurantiaca* had large calyces with floral tubes included at anthesis, reduced lower labia, and enlarged galea openings. *Pedicularis densiflora* had short calyces with fully exerted floral tubes, enlarged lower labia, and smaller galea openings. Taxonomy, phenology, and floral differences are discussed in the context of previously published data on pollinator visitation.

Key Words: California Flora, Morphological Variation, Oregon Flora, Orobanchaceae, *Pedicularis aurantiaca*, *Pedicularis densiflora*.

Pedicularis L. (Orobanchaceae, formerly Scrophulariaceae) is a large (approximately 500 species), monophyletic genus of hemiparasitic herbs, with a northern temperate distribution and tremendous diversity in floral morphology (Rec 2005). The genus has undergone a relatively recent diversification, likely in the Pleistocene, and shares a center of diversity in eastern Asia with its primary pollinator, *Bombus* (De-Yaun 1983). Considerable research has investigated the reproductive biology of *Pedicularis* and documented the modes of plant-pollinator interaction (e.g., Sprague 1962; Grant 1966; Grant and Grant 1967; Macior 1973, 1977, 1982, 1983, 1984, 1986a, b, 1995a, b, 1996, 1997 and references therein; Wang 1998a, b; Robart 2005).

Pedicularis densiflora Benth. ex Hook., a species found only in California and southern Oregon, was first described from a communication with Douglas by Bentham, and published by J. W. Hooker (1838). Sprague (1958) proposed dividing the taxon into two subspecies, *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca* E. F. Sprague. Her subspecific circumscriptions were based on distribution, reproductive biology, phenology, host affinity, and floral morphology (Sprague 1958, 1960, 1961, 1962).

According to Sprague (1958), *P. densiflora* subsp. *densiflora* is pollinated by both *Bombus* and hummingbirds while *P. densiflora* subsp. *aurantiaca* is pollinated exclusively by hummingbirds. Macior (1986a) documented pollinator

type, frequency, and mode of pollination of both subspecies. Macior's (1986a) research supported Sprague's (1958, 1962) conclusion that the subspecies have different pollination systems. Sprague (1962) and Macior (1986a) suggested that hummingbird pollination was driving a change in morphology among populations and creating a shift from a bumblebee pollination syndrome to a hummingbird syndrome.

There have been no detailed quantitative morphological studies to document the morphological divergence among the populations. There has been no attempt to relate morphological variation to the different pollinator systems in the two subspecies. An extensive examination was undertaken to detect and explain patterns of infraspecific variation among populations of the two subspecies.

MATERIALS AND METHODS

Herbarium Specimens

A total of 1069 herbarium specimens of *Pedicularis densiflora* subsp. *densiflora*, *P. densiflora* subsp. *aurantiaca*, and *P. semibarbata* A. Gray from CAS, DS, JEPS, K, MSC, ORE, OSC, POM, RSA, UC, and WILLU were studied. Specimens were examined to locate population study sites and identify morphological characters for measurement. Additional retrospective analyses of herbarium specimens were

TABLE 1. LIST OF POPULATIONS AND VOUCHER SPECIMENS FOR FLORAL MORPHOLOGICAL ANALYSIS OF *PEDICULARIS DENSIFLORA* SUBSP. *DENSIFLORA* AND *P. DENSIFLORA* SUBSP. *AURANTIACA*. All voucher specimens are deposited at Michigan State University Herbarium (MSC)

Species	Location (County, State)	Voucher
<i>P. aurantiaca</i>	Inskip (Butte Co., CA) N 39°59.541', W 121°32.389', 1309 m	Monfils 37
<i>P. aurantiaca</i>	McBride Springs (Siskiyou Co., CA) N 41°20.687', W 122°16.506', 1500 m	Monfils 43
<i>P. aurantiaca</i>	Pinehurst (Jackson Co., OR) N 42°07.452', W 122°20.783', 1167 m	Monfils 40
<i>P. densiflora</i>	Bear Valley (Colusa/Lake Co., CA) N 39°09.504', W 122°28.778', 810 m	Monfils 33
<i>P. densiflora</i>	Hurles Circle (Butte Co., CA) N 39°29.764', W 121°22.632', 625 m	Monfils 35
<i>P. densiflora</i>	Missouri Flats Road (Josephine Co., OR) N 42°19.288', W 123°13.871', 1188 m	Monfils 36
<i>P. densiflora</i>	Mount Diablo (Contra Costa Co., CA) N 37°51.814, W 121°55.770', 777 m	Monfils 28
<i>P. densiflora</i>	Paradise (Marin Co., CA) N 37°53.329', W 122°26.954', 33 m	Monfils 34
<i>P. densiflora</i>	Round Valley Historical Marker (Mendocino Co., CA) N 39°43.749', W 123°15.112', 658 m	Monfils 32
<i>P. densiflora</i>	Santa Margarita Lake (San Luis Obispo Co., CA) N 35°17.214, W 120°28.659', 670 m	Monfils 21

conducted to evaluate utility and reliability of the morphological traits used to distinguish the two subspecies, and to comprehensively review the distribution of the two taxa. Each specimen was examined and key diagnostic features were assessed to determine subspecies identification. After herbarium specimens were examined and identified, distribution, elevational range, and phenological data were gathered.

Analysis of Floral Morphological Variation

Study populations were selected from throughout the range of *Pedicularis densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*, sampling a broad elevational (30 to 1500 m) and geographic spectrum. Populations were chosen to represent the full breadth of morphological diversity previously described within *P. densiflora* (Sprague 1958, 1960, 1961, 1962). During a preliminary field season in 1998, sixteen localities were screened and ten populations were chosen for the study of floral morphological divergence. Populations were selected prior to measurement or subspecific determination. Population choice was based on population size and feasibility of using the site. Several populations located in the southern part of the range were peripheral populations consisting of few (3+) or scattered plants and could not be used to represent morphological variability. The Auberry Road population in the Southern Sierra Nevada Mountains was inaccessible for study after the initial field season due to weather and road conditions. Plants from these southern populations were vouchered and collections were

retroactively studied. Populations used in the morphological study were from the following ten localities: Bear Valley (Colusa/Lake Co., CA), Hurles Circle (Butte Co., CA), Inskip (Butte Co., CA), McBride Springs (Siskiyou Co., CA), Missouri Flats Road (Josephine Co., OR), Mount Diablo (Contra Costa Co., CA), Paradise (Marin Co., CA), Pinehurst (Jackson Co., OR), Round Valley Historical Marker (Mendocino Co., CA), and Santa Margarita Lake (San Luis Obispo Co., CA). Voucher specimens were deposited in the Michigan State University Herbarium (MSC; Table 1, Fig. 1A and B).

When available, 50 individuals per population were studied. A total of 466 flowers were measured. Within each population, one flower each was removed from each of 50 plants. Plants were selected by sampling at set intervals along transects encompassing the population. Intervals were selected to systematically study plants throughout the population. Floral measurements were made on the most apical flowers that were intact, fully developed, with an exerted stigma, and shedding pollen.

Measurements were made using digital calipers and recorded to the nearest 0.01 mm. Floral characters were selected based on the characters used by Sprague (1958) to differentiate the subspecies, determined by Macior (1986a) to be involved in effective pollination, and suggested by Faegri and Van der Pijl (1966) to be associated with *Bombus* and hummingbird pollination syndromes. Thirteen quantitative characters were measured and/or calculated: galea width (measured as width of laterally compressed galea), tube width (measured as width of laterally

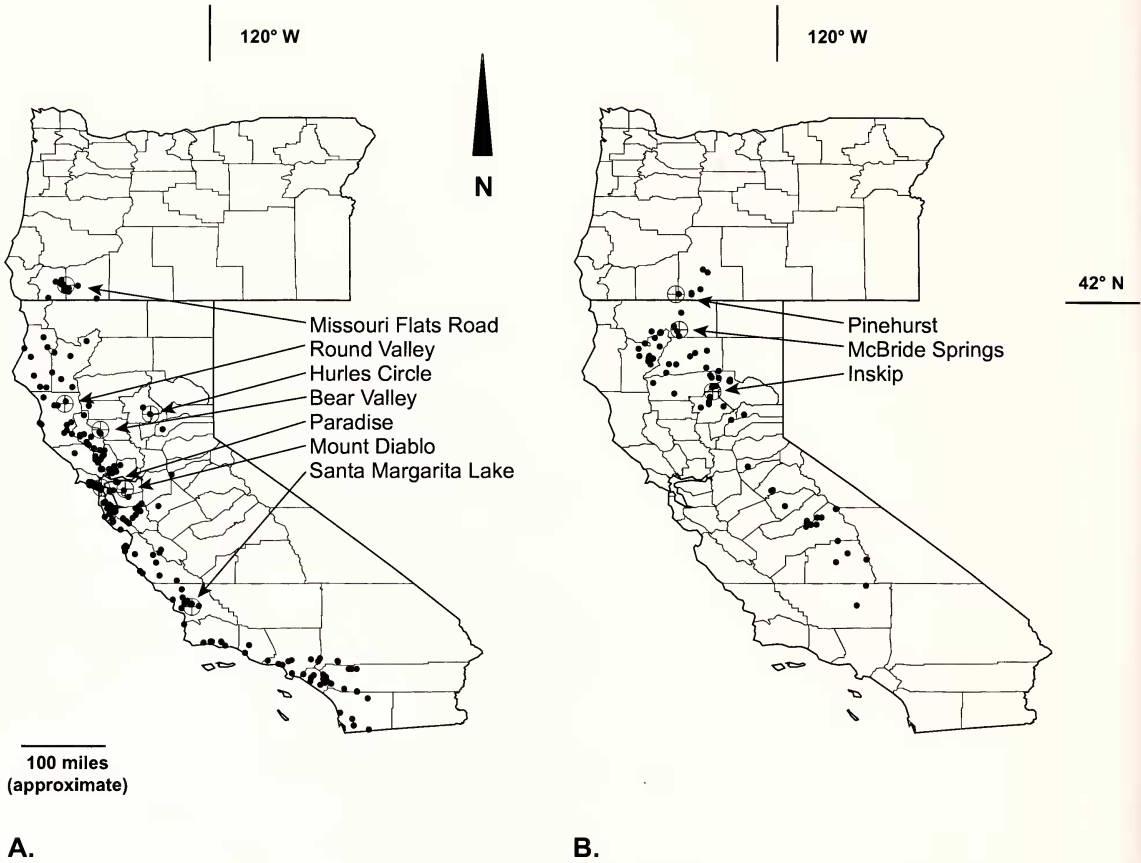


FIG. 1. A. Distribution of population study sites and herbarium specimens of *Pedicularis densiflora* subsp. *densiflora* (Baja California, Mexico site not shown). B. Distribution of population study sites and herbarium specimens of *Pedicularis densiflora* subsp. *aurantiaca*. Herbarium specimen localities determined when possible by GEOLocate (Tulane University Museum of Natural History, Belle Chase, LA). Dot indicates locality and may represent multiple specimens.

compressed tube), galea length, tube length, orifice width (measured as abaxial margin of galea), calyx length, pistil length, stamen length, labium length, axis angle (calculated from the galea length, tube length and length from galea tip to tube/receptacle junction), tube exertion (calculated by subtracting tube length from calyx length), corolla length (calculated by adding tube and galea length), and labium tip to galea bend length (Fig. 2). Four additional characters were ratios derived from the initial measurements and used to quantify the relationship between shape and size: orifice width/galea length, labium length/galea length, tube length/galea length, and tube width/galea width.

Statistical Analysis

The JMP statistical package (SAS Institute Inc., Cary, NC) was used to perform a non-hierarchical analysis among population means for all 13 quantitative floral morphological

characters using principal component analysis (PCA). Ratios derived from initial measurements were not included in the multivariate analysis to avoid spurious correlations (Atchley et al. 1976; Frampton and Ward 1998; Brett 2004). All measurements were standardized across the populations with a mean of zero and a variance of one. Varimax factor rotation (Kaiser 1958) was conducted using 13 rotated factors (Johnson and Wichern 2002).

A dissimilarity matrix was created from the 13 standardized quantitative floral morphological character traits with the program NTSYSpc version 2.1 (Applied Biostatistics, Inc. Setauket, NY) using the average “taxonomic” distance coefficient. The unweighted pair-group method of cluster analysis (UPGMA) was performed on the dissimilarity matrix, and a UPGMA phenogram was constructed.

Analysis of variance (ANOVA) was performed on all 17 characters for the ten populations using the SAS V8 (SAS Institute Inc., Cary, NC). The

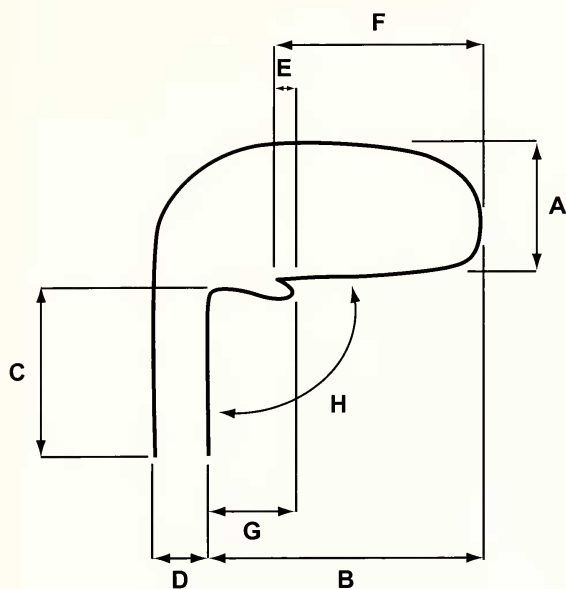


FIG. 2. Schematic representation of *Pedicularis densiflora* corolla. Lines represent parameters of quantitative measurements and letters correspond to the following measurements: A. galea width, B. galea length, C. tube length, D. tube width, E. labium length, F. orifice width, G. labium tip to galea bend length, and H. axis angle.

PROC UNIVARIATE and HOVTEST=LEVENE tests were conducted to test normality and homogeneity of variance, respectively. Where necessary, data were log, square root, or arcsine transformed to better fulfill the assumptions of standard variance and normality. Bonferroni (Dunn) t-tests were conducted on each variable to examine differences between all possible pairs of means and significant groupings among means for all ten populations.

RESULTS

Based on the PCA analysis, greater than 94% of the variance in the data set was explained by the first three factors. Factor one explained 46% of the variation and was weighted at 0.85 or higher for galea width, tube width, orifice width, calyx length, tube exertion, and labium tip to galea bend length. All these features corresponded to floral shape. Factor two explained 39% of the variation and was weighted at 0.85 or higher for tube length, pistil length, stamen length, and corolla length. These floral characteristics were predominantly attributed to flower size. Factor three explained 9% of the variation in the data set and was not weighted at 0.85 or higher for any of the 13 variables (Table 2).

In the factor by factor analysis of the varimax rotated principal components for the first three factors, factor one clearly separated two distinct clusters of populations: one group consisting of *P. densiflora* subsp. *aurantiaca* populations and a second cluster of *P. densiflora* subsp. *densiflora* populations (Fig. 3). Factors two and three produced a continuum of values which did not separate the populations into any discernable clusters.

The UPGMA phenogram summarized phenotypic similarities among populations. Separation of the populations into two distinct groups was substantiated by the phenogram, which showed high similarity among the *P. densiflora* subsp. *aurantiaca* populations. The seven populations of *P. densiflora* subsp. *densiflora* were also more similar to each other than they were to the populations of *P. densiflora* subsp. *aurantiaca* (Fig. 4).

All seventeen floral morphological variables (ratios included) showed significant differences among population means ($P < 0.05$) in the ANOVA. Examination of population means

TABLE 2. VARIMAX ROTATED FACTOR PATTERNS OF 13 FLORAL MORPHOLOGICAL TRAITS FOR PCA FACTORS 1-3 OF TEN POPULATIONS OF *PEDICULARIS DENSIFLORA* SUBSP. *DENSIFLORA* AND *P. DENSIFLORA* SUBSP. *AURANTIACA*. The first row shows proportion of variance explained by the first three factors. Varimax rotated factor patterns for the first three factors are listed next to the floral morphological traits.

	Factor 1	Factor 2	Factor 3
Proportion of variance explained by factor	46%	39%	9%
Rotated factor pattern for varimax rotation method			
Galea width	0.936551	0.314562	0.019986
Tube width	0.873642	0.463500	0.09779
Galea length	0.512363	0.710828	0.191500
Tube length	-0.068533	0.917692	0.284838
Orifice width	0.852061	0.425776	-0.217437
Calyx length	0.889926	0.152248	0.123741
Pistil length	0.062068	0.965496	-0.186622
Stamen length	0.201367	0.963109	0.088532
Labium length	-0.814386	0.281443	0.409147
Axis angle	-0.378592	0.542948	0.687267
Tube exertion	-0.924260	0.301912	0.217005
Corolla length	0.158965	0.939896	0.289686
Labium tip to galea bend length	-0.900535	-0.071308	0.405407

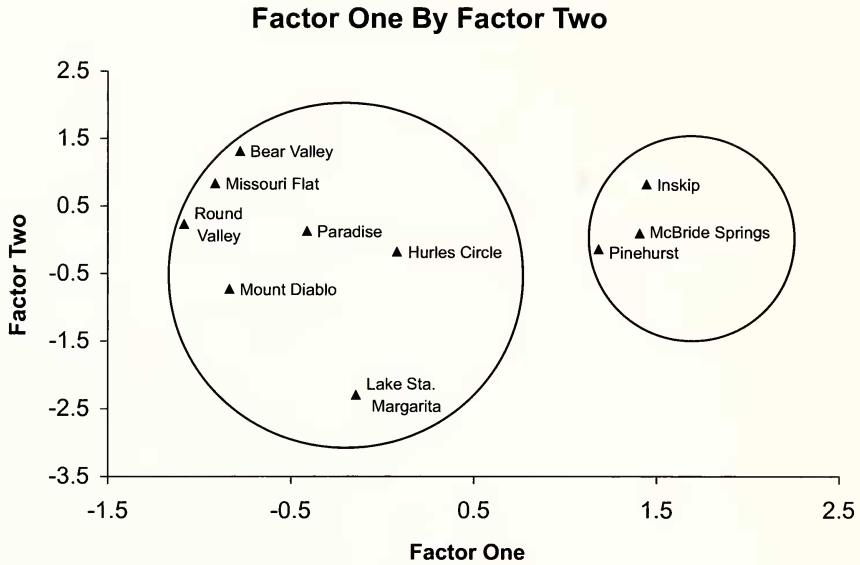


FIG. 3. Plot of factor one by factor two from the varimax rotated principal component analysis of 13 floral morphological characters in ten populations of *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. Large ellipse represents populations of *P. densiflora* subsp. *densiflora*; small ellipse represents populations of *P. densiflora* subsp. *aurantiaca*.

using the Bonferroni (Dunn) t-tests indicated the *P. densiflora* subsp. *aurantiaca* populations had means not significantly different from each other, but distinct from all populations of *P. densiflora* subsp. *densiflora* for five variables: galea width, orifice width, labium length, orifice width/galea length, and labium length/galea length. Two additional variables (calyx length and labium tip to galea bend) were found to be significantly different between *P. densiflora* subsp. *aurantiaca* and *P. densiflora* subsp. *densiflora*, but the Bonferroni (Dunn) t-tests found statistically different means among *P. densiflora* subsp. *aurantiaca* populations. An examination of the means, and minimum and maximum measurements showed these two characters could also be used to differentiate the populations of *Pedicularis densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. *Pedicularis densiflora* subsp. *aurantiaca* populations had large mean calyx lengths (≥ 17 mm) which were larger and significantly different from the *P. densiflora* subsp. *densiflora* populations (all ≤ 14 mm). In the case of mean labia tip to galea bend length, the *P. densiflora* subsp. *aurantiaca* populations had the lowest mean values (≤ 6 mm) which were significantly different from the *Pedicularis densiflora* subsp. *densiflora* populations with mean measurements ≥ 10 mm (Table 3).

Herbarium specimens and field observations provided data on phenology, elevational range and distribution of the two subspecies. *Pedicularis densiflora* subsp. *aurantiaca* flowers from late April through June and grows at elevations between 600 and 2100 m, with one exception

growing at 150 m. *Pedicularis densiflora* subsp. *aurantiaca* is distributed in southeast Oregon in Klamath and Jackson Counties, northern California in the Trinity and Siskiyou Alps, the western slopes of the Sierra Nevada, and as far south as Kern County (Fig. 1B). *Pedicularis densiflora* subsp. *densiflora* flowers from February through April and grows at elevations ranging from 30–1200 m. *Pedicularis densiflora* subsp. *densiflora* is distributed along the coast from southern Oregon to southern California with occurrences as far south as northern Baja California, Mexico. Populations occur in the foothills of the Sierra Nevadas in Butte, Calaveras, and Nevada counties (Fig. 1A). Both subspecies occur in Jackson County in Oregon, and Butte and Trinity Counties in California. Based on field observations and herbarium records the two species do not overlap in population localities, altitude, or flowering time in the three counties where they co-occur (Fig. 1A and B).

DISCUSSION

Herbarium specimens and field collections revealed two series of populations that are morphologically distinct from each other, and correspond to the circumscriptions of the two subspecies *P. densiflora* subsp. *aurantiaca* and *P. densiflora* subsp. *densiflora*. Populations within each series are morphologically cohesive. Based on geographic distribution, altitude and flowering time, *Pedicularis densiflora* subsp. *aurantiaca* is prezygotically isolated from *P. densiflora*

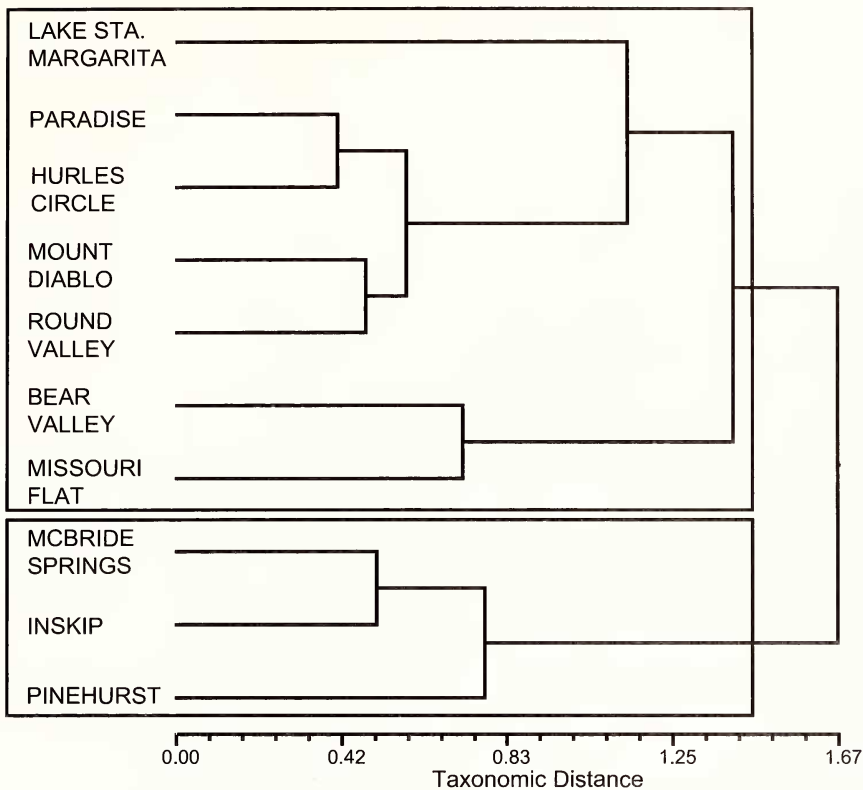


FIG. 4. UPGMA phenogram of taxonomic distance based on 13 continuous floral morphological character traits in populations of *P. densiflora* subsp. *densiflora* and *P. densiflora* subsp. *aurantiaca*. Population names, locations, and voucher information are described in Table 1. Large rectangle represents populations of *P. densiflora* subsp. *densiflora*; small rectangle represents populations of *P. densiflora* subsp. *aurantiaca*.

subsp. *densiflora*. *Pedicularis densiflora* subsp. *aurantiaca* was morphologically distinct, had a later growing season, and typically grew at higher elevations than *P. densiflora* subsp. *densiflora*. Where the two subspecies co-occur in Jackson County in Oregon, and Butte and Trinity Counties in California, *P. densiflora* subsp. *aurantiaca* flowers later than *P. densiflora* subsp. *densiflora* and at higher elevations. Morphological and ecological character traits are sufficiently different to merit species status and *P. densiflora* should be more narrowly circumscribed and *P. densiflora* subsp. *aurantiaca* should be elevated to species status.

The new combination is made below, and brief descriptions of the characters that may be used in differentiating the species *Pedicularis densiflora* and *Pedicularis aurantiaca* along with a key are provided.

Pedicularis aurantiaca (E. F. Sprague) Monfils & Prather, comb. et stat. nov. *Pedicularis densiflora* subsp. *aurantiaca* E. F. Sprague, Aliso, 4:130. 1962. Type: USA: from a burn in manzanita brush, Yellow Pine Forest, between the campground and the forest, Lake Almanor, Plumas County, California, at 4300 ft, 30

May 1957, E. F. Sprague 1202 (holotype: RSA; Isotype RSA!)

Description: Calyx tube 12–24 mm long. Corolla 23–43 mm, deep red to purple to orange-yellow, galea 14–26 mm long, 4–8 mm deep, orifice width 13–23 mm long, lower labium lobes 3–7 mm long from bend in corolla to petal tips. Corolla tube not exerted at anthesis.

600–2100 m. Flowers April through June. Additional Material seen in Appendix I

Pedicularis densiflora Benth. ex. Hook. Fl. Bor. Am. ii. 110. 1838. Type: Douglas s.n. 1833 (K—4 specimens; photos MSC!).

Synonym: *P. attenuata* Benth. Prodr. (DC.) x. 574. 1846. Isotype: Coulter s.n. (NY, On-line photo!)

Description: Calyx tube 10–18 mm long. Corolla 23–43 mm, deep red to purple to orange-yellow, sometimes white, galea 15–25 mm long, 4–7 mm deep, orifice width 9–20 mm long, lower labium lobes 8–16 mm long from bend in corolla to petal tips. Corolla tube exerted at anthesis.

30–1200 m. Flowers February through April. Additional Material seen in Appendix II

TABLE 3. CONTINUED

Character	Lake Santa Margarita (n = 19)	Paradise (n = 50)	Mount Diablo (n = 46)	Bear Valley (n = 50)	Round Valley (n = 51)	Hurles Circle (n = 51)	Missouri Flats Road (n = 50)	McBride Springs (n = 50)	Pinehurst (n = 50)	Inskip (n = 50)
Orifice width/ Mean (SD)	0.60 (0.05)	0.65 (0.04)	0.66 (0.07)	0.64 (0.05)	0.65 (0.04)	0.68 (0.05)	0.70 (0.05)	0.86 (0.03)	0.89 (0.03)	0.87 (0.03)
Galea Range	0.53-0.67	0.55-0.72	0.57-1.07	0.52-0.75	0.58-0.73	0.53-0.79	0.62-0.96	0.79-0.95	0.82-0.96	0.78-0.94
Length†	E	C D	C D	D	C D	B C	B	A	A	A
Labium Mean (SD)	0.205 (0.058)	0.216 (0.045)	0.276 (0.073)	0.270 (0.063)	0.242 (0.052)	0.226 (0.042)	0.275 (0.071)	0.141 (0.034)	0.141 (0.035)	0.152 (0.044)
Length/ Range	0.060-0.297	0.097-0.360	0.166-0.655	0.167-0.525	0.150-0.378	0.147-0.341	0.188-0.690	0.069-0.214	0.060-0.201	0.079-0.239
Galea Length	B	B	A	A	A B	B	A	C	C	C
Tube Length/ Mean (SD)	0.548 (0.096)	0.677 (0.081)	0.629 (0.079)	0.777 (0.115)	0.653 (0.080)	0.682 (0.071)	0.682 (0.111)	0.634 (0.084)	0.586 (0.072)	0.696 (0.127)
Galea Range	0.365-0.744	0.533-0.840	0.479-0.824	0.548-1.106	0.488-0.878	0.489-0.877	0.497-0.977	0.491-0.827	0.437-0.757	0.364-1.042
Length	E	B C	C D	A	B C	B C	B C	B C D	D E	B
Tube Width/ Mean (SD)	0.606 (0.056)	0.605 (0.060)	0.589 (0.056)	0.642 (0.072)	0.633 (0.063)	0.611 (0.059)	0.654 (0.070)	0.639 (0.062)	0.618 (0.056)	0.664 (0.078)
Galea Range	0.474-0.694	0.445-0.739	0.489-0.713	0.481-0.835	0.509-0.762	0.479-0.771	0.501-0.806	0.494-0.747	0.504-0.733	0.466-0.921
Width	C D	C D	D	A B C	A B C D	B C D	A B	A B C	B C D	A

Based on the data from the multivariate analysis and ANOVA, and confirmed by observation from 1069 herbarium specimens and field studies several traits are characteristic of *Pedicularis densiflora* and *P. aurantiaca*. Both species are pubescent several-stemmed perennials that grow in diffuse patches, with woody roots and haustoria preferentially parasitizing woody plants. Their leaves are petiolate, oblanceolate, bipinnate to pinnate, and grow in basal rosettes, with alternate branching on the peduncle. The inflorescence of both species is a raceme with flowers subtended by leafy bracts and the flowers have a five lobed calyx and a galeate corolla.

The two species, however, differ in several key character traits. *Pedicularis aurantiaca* has calyces 12-24 mm long and lower labia extending <8 mm from the tip to the galea bend, with the detached portion of the labia 1-5 mm long. The orifice widths are approximately 7/8^{ths} the length of the upper galea, and the detached lower labium to upper galea length ratio is approximately 1:7. Floral tubes are included in the calyx. *Pedicularis densiflora* has calyces 10-18 mm long and lower labia >8 mm from the tip to the galea bend, with the detached portion of the labia 2-12 mm long. The orifice widths are approximately 2/3 the length of the upper galea and the detached lower labium to upper galea length ratio is approximately 1:4. Floral tubes are exerted from the calyx (Fig. 5).

Previous work by Sprague (1958, 1960, 1962) and Macior (1986a) on variation in pollination indicates exclusive pollination by hummingbirds in *P. aurantiaca* and pollination by bumblebees and hummingbirds in *P. densiflora*. Long corolla tubes, abundant nectar, lack of floral scent, and red coloration were floral traits present in *P. densiflora* and *P. aurantiaca* which have an association with hummingbird pollinators (Sprague 1960; Grant & Grant 1968; Faegri and van der Pijl 1966). In *P. densiflora*, young flowers are visited by *Bombus* pollinators before the floral tubes are fully exerted and while the nectar is accessible to the short-tongued pollinators (Macior 1986a). The lower labium of *P. densiflora* was larger and capable of serving as a landing platform for *Bombus* pollinators. In *P. aurantiaca*, the calyx was larger and supported the corolla tube. This trait could serve to protect the ovary during the nectar probing of hummingbird visitation (Faegri and van der Pijl 1966). The labium was also significantly smaller and the orifice width larger in *P. aurantiaca* than in *P. densiflora* flowers. The smaller lower labium in *P. aurantiaca* flowers possibly makes it difficult for *Bombus* pollinators to land and the enlarged orifice width can accommodate the larger head of the hummingbird pollinators.

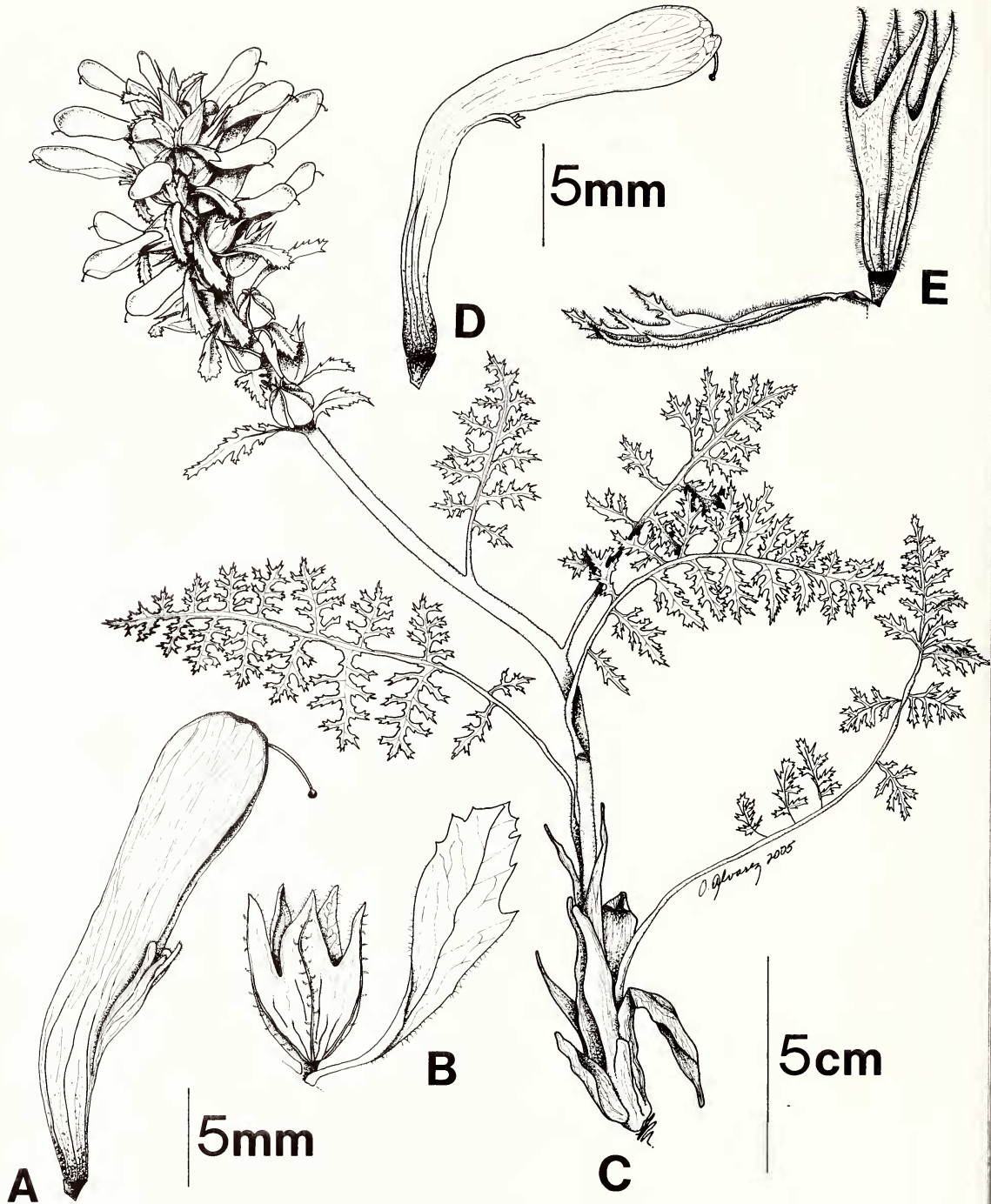


FIG. 5. A. Mature flower minus calyx of *Pedicularis densiflora*. B. Calyx of *P. densiflora*. C. Mature plant of *P. aurantiaca*. D. Mature flower minus calyx of *P. aurantiaca*. E. Calyx of *P. aurantiaca*. Voucher associated with *P. densiflora* - Monfils 13 (MSC). Voucher associated with *P. aurantiaca* - Monfils 40 (MSC).

KEY:

Corolla \pm club-like, upper labium hooded, not beaked; lower labium not fan-like

Corolla deep red to red-purple (or yellow to orange, occasionally white), lower labium $<1/2$ upper

Lower labium ≥ 8 mm. Galea opening $>4/5$ th the length of galea. Tube exerted beyond the calyx lobes at anthesis. *Pedicularis densiflora*

Lower labium < 8 mm. Galea opening $<4/5$ th the length of galea. Tube inserted in the calyx lobes at anthesis *Pedicularis aurantiaca*

ACKNOWLEDGMENTS

We wish to thank Orlando Alvarez-Fuentes for botanical illustrations, Larry Burditt and Mike Monfils for assistance with figures, and John C. Hunter, Steve O'Kane and an anonymous reviewer for constructive comments. This research was funded by the following sources: Botanical Society of America, California Native Plant Society, Ecology, Evolutionary Biology and Behavior Program (Michigan State University; MSU), Paul Taylor Funds (Department of Plant Biology, MSU), Oregon Native Plant society, and Sigma XI. We also thank the herbaria listed in the text for making specimens available for study. This work was conducted in partial fulfillment of a doctoral dissertation in the Department of Plant Biology at Michigan State University.

LITERATURE CITED

- ATCHLEY, W. R., C. T. GASKINS, AND D. ANDERSON. 1976. Statistical properties of ratios. I. Empirical results. *Systematic Zoology* 25:137-148.
- BRETT, M. T. 2004. When is a correlation between non-independent variables "spurious"? *Oikos* 105:647-656.
- DE-YAUN, H. 1983. The distribution of Scrophulariaceae in the holoarctic with special reference to the floristic relationships between Eastern Asia and Eastern North America. *Annals of the Missouri Botanical Garden* 70:701-712.
- FAEGRI, K. AND L. VANDER PIJL. 1966. The principles of pollination ecology, 1st ed. Pergamon Press, Oxford.
- FRAMPTON, C. M. AND J. M. WARD. 1999. The use of ratio variables in systematics. *Taxon* 39:586-592.
- GRANT, K. A. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. *American Naturalist* 100:85-97.
- AND V. GRANT. 1967. Effects of hummingbird migration on plant speciation in the California flora. *Evolution* 21:457-465.
- AND —. 1968. Hummingbirds and their flowers. Columbia University Press, New York, NY.
- HOOVER, J. W. 1838. *Flora Boreali-Americana*. Vol. 2. Hafner Publishing Co., NY. p. 110.
- JOHNSON, R. A. AND D. W. WICHERN. 2002. Applied multivariate statistical analysis, 5th ed. Prentice Hall, Upper Saddle River, NJ.
- KAISER, H. F. 1958. The varimax criterion for analytical rotation in factor analysis. *Psychometrika* 23:187-200.
- MACIOR, L. W. 1973. The pollination ecology of *Pedicularis* on Mount Rainier. *American Journal of Botany* 60:863-871.
- . 1977. The pollination ecology of *Pedicularis* (Scrophulariaceae) in the Sierra Nevada of California. *Bulletin of the Torrey Botanical Club* 104:148-154.
- . 1982. Plant community and pollinator dynamics in the evolution of pollination mechanisms in *Pedicularis* (Scrophulariaceae). Pp. 29-45 in J. A. Armstrong, J. M. Powell, and A. J. Richards, (eds.), *Pollination and evolution*. Royal Botanic Gardens, Sydney, Australia.
- . 1983. The pollination dynamics of sympatric species of *Pedicularis* (Scrophulariaceae). *American Journal of Botany* 70:844-853.
- . 1984. Behavioral coadaptation of *Bombus* pollinators and *Pedicularis* flowers. V^{ème} Symposium International sur la Pollinisation. Versailles 27-30 Septembre 1983. Ed. INRA Publ. (Les Colloques de l'INRA, n-21).
- . 1986a. Floral resource sharing by bumblebees and hummingbirds in *Pedicularis* (Scrophulariaceae) pollination. *Bulletin of the Torrey Botanical Club* 113:101-109.
- . 1986b. Pollination ecology and endemic adaptation of *Pedicularis howellii* Gray (Scrophulariaceae). *Plant Species Biology* 1: 163-172.
- . 1995a. Pollination ecology of *Pedicularis* in the Teton Mountain region. *Plant Species Biology* 10:77-82.
- . 1995b. Pollination ecology of *Pedicularis parryi* subsp. *purpurea* (Parry) Carr (Scrophulariaceae). *Plant Species Biology* 10:163-168.
- . 1996. Pollination ecology of *Pedicularis bracteosa* in the montane-subalpine ecotone. *Plant Species Biology* 11:165-171.
- AND T. YA. 1997. A preliminary study of the pollination ecology of *Pedicularis* in the Chinese Himalaya. *Plant Species Biology* 12: 1-7.
- REE, R. H. 2005. Phylogeny and the evolution of floral diversity in *Pedicularis* (Orobanchaceae). *International Journal of Plant Science* 166:595-613.
- ROBART, B. W. 2005. Morphological diversification and taxonomy among the varieties of *Pedicularis bracteosa* Benth. (Orobanchaceae). *Systematic Botany* 30:644-656.
- SPRAGUE, E. F. 1958. A new subspecies of *Pedicularis densiflora*. *Aliso* 4:130.
- . 1960. Ecological life history of California species of *Pedicularis*. Ph.D. dissertation. Claremont Graduate School, Claremont, CA.
- . 1961. Parasitism in *Pedicularis*. *Madroño* 16:192-200.
- . 1962. Pollination and evolution in *Pedicularis* (Scrophulariaceae). *Aliso* 5:181-209.
- WANG, H. 1998a. A preliminary study of pollination biology of *Pedicularis* (Scrophulariaceae) in northwest Yunnan, China. *Acta Botanica Sinica* 40:204-210.
- . 1998b. The pollination syndrome of *Pedicularis rex* (Scrophulariaceae) and its biogeographical significance. *Acta Botanica Sinica* 40:781-785.

APPENDIX I
 ADDITIONAL MATERIAL SEEN *PEDICULARIS*
AURANTIACA

Additional material seen: UNITED STATES. Oregon: Jackson County: 1–1.5 mi past Pinehurst Inn. N 42°07.452', W 122°20.783', 1167 m, 24 May 1998, *Monfils 12* (MSC); 1–1.5 mi east of Pinehurst Inn. N 42°07.461', W 122°20.756', 1131 m, 11 May 2000, *Monfils 40* (MSC); Pinehurst, 20 Jun 1927, *Peck 15044* (DS, WILLU); Pinehurst, 27 May 1948, *Peck 24973* (WILLU, UC); Near Pinehurst, 1219 m, 13 Apr 1934, *Thompson 10347* (CAS, DS, POM, WILLU). Klamath County: Cascade Mnts. Near Long Prairie, along old Klamath Falls-Ashland road, 15 Jun 1895, *Applegate 421a* (DS); Southeast of Topsy, 1372 m, 12 May 1898, *Applegate 2059* (DS); Top of Spencer Mt., Cascade Mts., 11 May 1924, *Applegate 4046* (DS, WILLU); Eastern Cascades, 30 Jun 1902, *Cusick 2851* (DS, ORE, POM); Klamath Falls Road "East of Mt.", 2 Aug 1925, *Henderson s.n.* (ORE); Along Ashland-Klamath Falls road, 18 mi W of Keno, May 1932, *Peck 9302* (DS, WILLU); Mts. Below Klamath Falls near Ore-Calif line, on Klamath River, May 1932, *Sprague s.n.* (OSC). County Unknown: Southern Oregon, 13 May 1907, *Henderson s.n.* (ORE); Location and date unknown, *Bellinger s.n.*, (WILLU). **California:** Amador County: Jackson, 12 Apr 1933, *Ball 18269* (RSA). Butte County: Colby, May 1890, *Austin 111* (UC); Jonesville, 16 Jun 1923, *Bassett s.n.* (CAS); Paradise, May 1898, *Bruce 2419* (DS, POM); Brush Creek, 1907, *Conger 453* (CAS, POM); Chico Meadows in the Sierra Nevada, 1219 m, 11 Jun 1915, *Heller s.n.* (DS); Stirling, 1073 m, 18 May 1919, *Heller 13170* (CAS,DS); Pentz Road, 3 mi below Paradise, 23 Mar 1939, *Heller 15358* (DS); DeSabra, 853 m, 18 Apr 1978, *Howell 52852* (CAS); Above the road between Paradise and Butte Meadows .1 mi. s. of Inskip. T25N, R.4E, sect. 33, 10 May 1981, *McNeal 2487* (OSC); Inskip on Skyway Road. Elevation N 39°59.541', W 121°32.389', 1309 m, 22 May 1998, *Monfils 6* (MSC); Inskip on Skyway Road. N 39°59.527', W 121°32.461', 1309 m, 9 May 2000, *Monfils 37* (MSC); Durham, 17 Apr 1932, *Morrison s.n.* (CAS). Fresno County: 5 mi east of Auberry, Big Sandy Bluff, 945 m, 19 Mar 1969, *Ahner s.n.* (CAS); Big Sandy Valley near the foot of ne. slope of Black Mt. Big Sandy Bluff beyond Ridge View Ranch which is across the road from my place, 610 m, 20 Mar 1953, *Carter 157* (CAS, UC); About 2 mi north of Kerckhoff Reservoir, 610 m, 29 May 1967, *McClintock, Roderick & Johnson s.n.* (CAS); Old fire trail road off Auberry Road. N 37°05.144', W 119°26.859', 1147 m, 20 May 1998, *Monfils 4* (MSC); R. R. Grade Rd. 1+ m. w. of jct. Hiway 168 at Shaver Xing between Shaver L. & Big Crk. 1st live crk. – small intake with pipe heading down crk. – Big Creek pentstocks in view. Heavy yellow pine for. 4500'–1000' up s. wall Big Crk. Canyon; 6830' Music Mt. Just sw; 8107' Black Pt. N. across canyon, San Joaquin R. at 2000' 4 map miles w., 17 Jun 1955, *Quibell 5102* (RSA); 5 mi east of Auberry, Big Sandy Bluff range, 945 m, 19 Mar 1969, *Shannon s.n.* (RSA); Scattered along Old Railroad Grade Road. R.23E., T9S., SW1/4 section 34, 853 m, 22 Mar 1980, *Shevlock 6819* (CAS, MSC); Taken near Fish Camp, 14 Apr 1938, *Whilton s.n.* (RSA); Along road from Shaver Lake to Big Creek Power House. W. slope of Sierra Nevada, 1829 m, 5 May 1929, *Wolf 3682* (RSA); 6 mi. above Auberry on road to Pineridge. W. slope of Sierra

Nevada [Editorial comment: Georeferenced in Madera County], 18 May 1933, *Wolf 4786* (CAS, RSA, UC). Kern County: Poso Creek narrows, below Poso Flat, 762 m, 9 Mar 1963, *Record 82-1* (CAS-2); Near mouth of South Fork Kern River Canyon, trail along Bartolas Creek, Domeland Wilderness, north of California highway 178 and NW of the Bloomfield Ranch R35E, T25S, section 23. Lat/Long: 35 degrees 44'45"N, 118 degrees 11'15"W., 1006 m, 20 Apr 1991, *Shevock 12026* (CAS); Back canyon at the cypress grove, 1265 m, 26 May 1964, *Twisselmann 950* (CAS-2). Mariposa County: Mariposa, 610 m, 10 Apr 1959, *Ballantyne 236* (CAS); Awahnee, 9–16 Apr 1926, *Shank 17471*, (RSA). Placer County: Tahoe Forest, Rebel ridge Range [Editorial comment: Georeferenced in Sierra County], 701 m, 12 Apr 1926, *Smith 53916* (CAS-2). Plumas County: Sw. shore Lake Almanor, 2 mi. s. of jct. of State Hwy. 89/36, 1402 m, 23 May 1957, *Balls 22519* (RSA, UC); 1 3/10 s. of Drakesbad, 3 Jul 1938, *Cantelow 2323* (CAS); Prattville, Summer 1906, *Coombs s.n.* (CAS); Woodleaf, 3000–4000', 14 Apr 1931, *Rose s.n.* (CAS, DS, POM, UC); Lake Almanor, 4300', 30 May 1957, *Sprague 1214* (RSA); Growing in dry loam in shade of *Libodendrus decurrens*. A low cool draw 6 mi south-west of Viola, 2800', 30 May 1957, *Sprague 1231* (RSA). Shasta County: Montgomery Creek, 18 Apr 1923, *Beltiel s.n.* (CAS); Near McBride Springs. On banks and under chaparral [Editorial comment: Georeferenced in Siskiyou County], 24 Jun 1938, *Cooke 11098*, (DS, OSC); Squaw Creek Ranger Station, Jun 1916, *Drew s.n.* (DS); Mt. Shasta [Editorial comment: Georeferenced in Siskiyou County], 21 Jun 1893, *Dudley s.n.* (DS); Burney Butte, 12 Jul 1912, *Eastwood 1034* (CAS); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], 20 May 1923, *Eastwood 11854* (CAS-2); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], 15 May 1918, *Herrin s.n.* (CAS); Shasta Springs [Editorial comment: Georeferenced in Siskiyou County], May 1922, *Herrin s.n.* (CAS); Open manzanita-oak association 3 mi east of Redding, 500', 17 May 1940, *Hitchcock 6466* (DS, POM); Highway 44, 5 mi west of Lassen National Park, 4600', 9 May 1974, *Keller 1301* (CAS). Siskiyou County: Bare serpentine gravel hillside, Scott Mnt. 8 mi above Callahan, 5150', 17 May 1954, *Barneby 11537* (CAS); Near Mt. Shasta, 6000–7000', 1–15 Jun 1897, *Brown 356* (DS); Alpina Mnts. Goosenest foothills, 5000', 10 May 1910, *Butler 1324* (DS, POM, UC); N. slope of Scott Mnt., 4000', 20 May 1936, *Cantelow 1435* (CAS); Scott Mountain campground, 10 mi S. of Callahan, 5350', 21 May 1949, *Constance, Bonar, Holm & Wood 3288* (UC); 0.8 mi N of Scott Mnt. Summit on Hwy 3. South Slope, 5200', 5 Jun 1975, *Davidson 2684*, (RSA); Bald mountain in road from Mt. Hebron to Montague, 5500', 15 May 1940, *Gould 1242* (DS); Mt. Eddy in open gravelly places in the forest, 6800', 15 Jul 1915, *Heller 12085* (CAS,DS, UC); Sugar Creek, Salomon Mountain Range, 5500', 26 May 1949, *Parker 257* (UC); Weed, 10 Apr 1913, *Smith 66* (CAS); Dunsmuir, 29 Apr 1913, *Smith 151* (CAS); Shady hillside near Weed, 28 Mar 1930, *Tebbe 61* (UC); Salmon Mnts., Klamath National Forest. Near South Fork of Salmon River, 5 to 9 mi southeast of Cecilville, between Lat. 41°03' and 41°06'N., and Long 122°58' and 123°03'W. Vicinity of Blind Horse Creek, 3000–3500', 13 May 1954, *Thomas 4129* (DS-2); Salmon-Trinity Mnts. about 6 mi SE of Cecilville. West side of Rush Creek, 3800–

4000', 21 Jul 1954, *Thomas & Thomas 4425* (DS); Mt. Shasta, McBride Springs. N 41°20.687', W 122°16.506', 4922', 11 May 2000, *Monfils 43* (MSC). Tehama County: Along road from Viola to Mineral, 9.5 mi south of Viola, 5000', 12 Jun 1962, *Breedlove 3423* (CAS, DS); Deer Creek Rd. (Rt. 32) at milepost 12, E side of Deer Creek ca 20 airmiles SW of Chester, 3200', 3 May 1989, *Erter 8435* (RSA); Mill Crk. Meadows, 6 Jun 1951, *Quick 51-93* (CAS); Northern Sierra Nevada. Red Bluff-Susanville Road, 3 6/10 mi. below Mineral, 4800', 17 May 1937, *Wolf 8712* (RSA). Trinity County: T35N, R11W, sect. 6. North fork of Trinity River, Hobo Gulch Camp and Vicinity, (18 mi NW of Weaverville) Along East Fork Trail, just over on the east side of Backbone Ridge, 4000', 25 Apr 1972, *Carter 374* (CAS-2); T36N, R11W, sect. 31. North fork of Trinity River, Hobo Gulch Camp and Vicinity, (18 mi NW of Weaverville) Along trail 0.1 mi north of Hobo Gulch. (Same location as 399-27 Apr. 72), 3100', 8 Jun 1972, *Carter 399.01*, (CAS-2); Scott Mnts. N. of Carrville, 25 Jun 1937, *Eastwood & Howell 5013* (CAS); 3 mi from Douglas City on Redding Road, 26 Apr 1954, *Howell 29164* (CAS); Dry open coniferous forest in Canadian Zone, Scott Mt. Summit on road from Carrville to Callahan, 5400', 20 May 1980, *Howell, Fuller & Barbe 53541* (CAS); Weaverville, Spring 1915, *Junkans s. n.* (CAS); Trinity Center, 30 Apr 1928, *Kildale 4605* (DS); Weaverville, 30 May 1931, *Kildale 10812* (DS); Foothills, Weaverville, 4000', 11 Apr 1880, *Kleiberger s. n.* (CAS); East Weaver Campground on East Weaver Creek Road. N 40°46.399', W 122°55.371', 4248', 23 May 1998, *Monfils 8* (MSC); Hobo Gulch. N 40°55.723', W 123°09.398', 4249', 23 May 1998, *Monfils 9* (MSC); East Weaver Public Camp, East Weaver Creek, 3000', 16 May 1949, *Munz 13256* (RSA); T32N, R9W, Secs. 28 & 33; Mt. Diablo Meridian; Southeast of confluence of Panwauket Gulch and Reading Creek; blue oak-pine woodland, 610 m, 18 May 1975, *Sullivan 88* (RSA); Little East Weaver Creek, 3000', 21 May 1914, *Yates 19370* (CAS). Tulare County: Mineral King, 2000', 11 Apr 1958, *Pawek 418* (DS); Occasional in recently disturbed road bank along Blue ridge, section 10, R.29E., T. 19S. South facing slope, 4900', 12 May 1979, *Shevock 6186* (CAS); Uncommon along Calif. Hwy 245, about one mile west from the junction with Dry Creek Road. R.27E., T. 15S. section 15, 2800', 11 Mar 1980, *Shevock 6775* (CAS); Lone Pine Spring, White River, 3350', 8 Mar 1940, *Smith 51*, (CAS). Tuolumne County: Priest Grade, near Big Oak Flat, Yosemite National Park, 20 Feb 1982, *Botti 1489* (CAS). Groveland. Woodland edge of route 120 about 4 mi east of town, 23 Apr 1974, *Churchill 744231* (MSC). Yuba County: Between Dobbins and Bullard Bar Dam, Watershed of North Fork of the Yuba River, 3.1 mi. e. of Dobbins (or 5.5 mi s.w. of Bullard Bar Dam), 2570', 19 Apr 1956, *Bacigalupi, Robbins & Chisaki 5622* (RSA); Comptonville, 7 Apr 1918, *Eastwood 6795* (CAS). County Unknown: Sterling City, 18 May 1935, *Whitaker s. n.* (OSC).

APPENDIX II

ADDITIONAL MATERIAL SEEN *PEDICULARIS*
DENSIFLORA

Additional material seen: UNITED STATES. **Oregon:** Jackson County: Thompson Creek, near Applegate, steep hill slope. sect. 21 T.38S R.4W, 1400', 19 Mar 1940, *Detling 3864* (ORE); Fls. Deep purple-red

open pine woods on alluvium, along Applegate River, 11/2 mi. s.e. of Provolt, 28 Apr 1948, *Glowenke 11113* (UC); 5 mi S of Applegate, under madronas, 1 Jun 1951, *Hitchcock 19395* (RSA); Applegate Creek, Mar 1921, *Leiberg s. n.* (ORE); Applegate R., Jacksonville, 27 Mar 1936, *Lund s. n.* (OSC); Pilot Rock, 20 Apr 1932, *Neiman s. n.* (WILLU); Woods along Thompson Cr. 5 mi. S. of Applegate P.O., 26 Jun 1931, *Peck 16423* (WILLU-2); Along the Applegate River, 12 Apr 1927, *Thompson 2225* (DS,ORE). Josephine County: 4 mi. N.W. of Provost, 25 Apr 1943, *Bellinger s. n.* (WILLU); 3 mi south of Grants Pass on New Hope Road, 9 May 1963, *Curtis s. n.* (OSC); Applegate Valley T37S R5W sect. 34, 21 Apr 1942, *Detling 5138* (ORE); In open woods, Fruitvale, 21 Apr 1930, *Henderson 12513* (ORE); Roadside in mixed Oak-Pseudotsuga woods; S. facing; on old river bench. 2 mi E of Murphy R5W; T37S; SE1/4 OF NW1/4, 345 m, 20 Apr 1968, *Lillico 426* (ORE); Missouri Flat Road. N 42°19.288', W 123°13.871', 3900', 24 May 1998, *Monfils 13* (MSC); Missouri Flat Road. N 42°19.288', W 123°13.871', 3900', 10 Apr 1999, *Monfils 36* (MSC); Applegate River, North Bank Road c. 1 mi. from Redwood Highway; S. of Grants Pass, 1300', 23 Apr 1967, *Pike 111* (ORE); Hillside near Grants Pass, 19 Mar 1918, *Prescott s. n.* (WILLU); Near Williams Creek highway between Provolt and Williams; also on N. side of Applegate River on Missouri Flat. Clayey soil in woods, 13 Apr 1924, *Savage s. n.* (ORE); Fruit Dale, Murphy Road. In open woods, 24 Mar 1926, *Savage s. n.* (ORE); Mixed woods near Takilma, 21 Apr 1930, *White s. n.* (ORE). **California:** Alameda County: Laundry Harm, 29 Jan 1895, *Cannon s.n.* (CAS); Oakland Hills, 28 Feb 1936, *Covel 371* (CAS); Laundry Harm, 26 Apr 1891, *Eastwood s.n.* (ORE); Mines Road s. w. of Livermore, near entrance to Rancho Los Mochos Boy Scout Camp, 1500', 3 Mar 1968, *Gagné s.n.* (CAS). Butte County: Near Hurlton, 1800', 26 Mar 1980, *Ahart 2060* (CAS); Cherokee mine, 29 Mar 1919, *Heller 13097* (CAS, DS, POM); Hurler Circle, in center island. N 39°29.764', W 121°22.632', 2050', 22 May 1998, *Monfils 5* (MSC); Hurler Circle, in center island. N 39°29.764', W 121°22.632', 2050', 7 Apr 1999, *Monfils 35* (MSC). Calaveras County: Comanche, 16 Apr 1939, *Hoover 4032* (CAS). Colusa County: Wilbur Springs. T15N, R6W, sect. 35, 3500', 14 Apr 1979, *Roth 9* (RSA); Along Brim Rd., 2.9 mi. W jct. Bear Valley Rd., 30 Mar 1996, *Vincent & Rhode 7304* (RSA). Contra Costa County: Martinez, 300', 18 Mar 1931, *Benson 2662* (POM); Mount Diablo, 17 Mar 1922, *Eastwood 11084* (CAS); Rocky Point, Mount Diablo, N 37°51.814, W 121°55.770', 2550', 22 Mar 1999, *Monfils 28* (MSC); Rocky Point, Mount Diablo, 2000', 5 Apr 1956, *Sprague 1096* (RSA); Mount Diablo, 2000', 11 Apr 1957, *Sprague 1124* (RSA); Rocky Point, Mount Diablo, 2000', 30 May 1957, *Sprague 1134* (RSA). Glenn County: 2 mi north of Alder Springs, 3900', 19 May 1949, *Munz 13330* (RSA). Humboldt County: T7N, R5E, sect. 29. Along highway 96, 1.9 mi north of Willow Creek, 1 May 1965, *Anderson 3556* (RSA); In damp fir woods near creek, Boise Creek and Willow Creek, Trinity River, 1 Apr 1947, *Brown 25* (DS); Philabiumsville, south fork of El River, 20 Mar 1927, *Kildale 2909* (DS); Briceland Bridge near Garberville, 375', 17 Apr 1925, *Kildale 3096* (DS, RSA); Briceland Road. N 40°05.678', W 123°51.222', 1874', 25 May 1998, *Monfils 14* (MSC); Round Valley Historical Marker. N 39°43.749', W 123°15.112', 2160', 25 May

- 1998, *Monfils 16* (MSC); Kneeland Prairie, in woods in ravine, 2500', 8 Jun 1908, *Tracy 2637* (UC); Vicinity of Garberville, 400', 17 Mar 1923, *Tracy 6160* (UC); Trinity River Valley, near the south fork, 600', 28 Feb 1926, *Tracy 7369* (UC); Hoopa Mnt., near summit on road west from Hoopa to Bair's, 3500', 15 May 1927, *Tracy 8060* (UC); Willow Creek Canyon, 2000', 26 Apr 1931, *Tracy 9340* (UC); Trinity River Valley, at Willow Creek, 500', 3 Apr 1937, *Tracy 15251* (UC); Trinity River Valley, at Willow Creek, 500', 26 Mar 1941, *Tracy 16818* (UC); Harris, in woods, 2500', 31 May 1948, *Tracy 18006* (UC). Lake County: Lakeport, 20 Apr 1917, *Bentley s. n.* (DS); Mt. Kelseyville, Middle N. Coast, Near Cold Creek Canyon River, 1700', 30 Mar 1928, *Benson 87* (POM); Bogg's Lake, Mt. Hanna, Middle N. Coast, Clear Lake watershed, 3500', 18 May 1935, *Benson 6636* (POM); Hannah, 3000', 8 Apr 1923, *Blankinship s. n.* (CAS); Mt. Konociti, 2000', 27 Mar 1926, *Blankinship s.n.* (RSA); Sulphur Banks, Apr 1902, *Bowman s. n.* (DS); E. of Middleton, 7 Apr 1940, *Cantelow 4346* (CAS); 4 mi. below Tollhouse on Middleton Road, 22 Feb 1924, *Duncan s. n.* (DS); Dasheills Mt., Sanhedrin, 23 May 1925, *Eastwood 12912* (CAS); Elk Mt., 17 May 1938, *Eastwood & Howell 5703* (CAS); Clear Lake, 14 Apr 1928, *Galloway s.n.* (CAS); Glenbrook, near Jordan Park, 30 Mar 1931, *Jussel 29* (CAS); Cobb Mt., 30 Mar 1931, *Jussel s. n.* (CAS); Cobb Mt., 31 Mar 1931, *Jussel s. n.* (CAS); Mt. St. Helena, 1 Apr 1933, *La Motte s. n.* (POM); Cobb Mt., 4 Jul 1893, *Leitholt s. n.* (DS); Bear Valley on Brim Road. N 39°09.504', W 122°28.778', 2665', 26 May 1998, *Monfils 17* (MSC); Bear Valley on Brim Road. N 39°09.431', W 122°28.798', 2180', 26 May 1998, *Monfils 33* (MSC); Butt's Cyn. Rd. near Middleton, 1000', 25 Mar 1972, *Shevock 1437* (RSA); Northeast facing slope, 0.4 mi southeast of Black Oak Villa in Butts Canyon, 1.1 mi from Lake-Napa county line on Pope Valley road, 800', 7 Mar 1953, *Sweeney 971* (UC); Chaparral 11 mi. S. of Lower Lake, 13 Mar 1932, *Wiggins 5769* (DS); 21/2 mi S. W. of Lakeport. sect. 34, T.14N, R.10W, 1850', 14 May 1937, *Wilson 376* (UC). Los Angeles County: Mts. above Claremont, Johnson Pasture, 15 Feb, *Bragg s. n.* (POM); North slope Sta. Monica Hills, Feb 1903, *Braunton 809* (DS, ORE-2); Topanga Canyon, 28 Mar 1929, *Clare s.n.* (RSA-2); Laurel Canyon, 24 Feb 1929, *Detruers s.n.* (RSA); Mulholland Drive, 6 Mar 1935, *MacFadden13246* (CAS); Laurel Canon, Mar 1943, *Merritt s.n.* (RSA); Franklyn Canyon, Santa Monica Mts., 21 Feb, *Peirson 1168* (RSA); Glendora, Little Dalton Trail, 16 Feb 1916, *Perkins s.n.* (RSA); 0.7 mi from Triunfo Canyon, 2 mi west of Cornell, Lobo Canyon, 800', 31 Mar 1959, *Thompson 1010* (CAS, RSA); Hwy. 23 south of Lake Elanor, Santa Monica Mtns., 1000', no date, *Wallace & Wilkin 150* (RSA). Marin County: East side of the Tiburon Peninsula just below the summit, 31 Mar 1981, *Best s. n.* (CAS); On trail 0.5 mi. above Phoenix Lake near jct. of Mt. Tamalpais trail, 1200', 5 Apr 1956, *Campbell 8* (RSA); Mount Tamalpais, 22 Feb 1901, *Chandler 760* (POM, UC); Old hardpacked fire road, 100', 9 Feb 1975, *Edelbrock 4*, (CAS); Summit Alpine Lake Trail above Deer Park, 8 Mar 1936, *Ewan 9408* (RSA); Summit Alpine Lake trail above Deer Park, 8 Mar 1936, *Ewan 9409* (UC); Mt. Tamalpais, 22 Apr 1930, *Forest s. n.* (RSA); Tamalpais T1N R6W, 600', 28 Mar 1935, *French 619* (UC); South side of Mt. Tamalpais, 7 Mar 1902, *Heller & Brown 5008* (DS, MSC, POM); Tiburon, 15 Feb 1938, *Hoover 2739* (UC); San Geronimo Ridge, 25 Feb 1940, *Howell 15388* (CAS); Carson Ridge, 19 Apr 1942, *Howell 16949A* (CAS-2); San Arseloro Canyon, 25 Feb 1940, *Howell s. n.* (CAS); Above Blythedale Canyon, east side of Mt. Tamalpais, 2 Mar 1947 *Howell s. n.* (CAS); Mill Valley, 29 Mar 1891, *Jepson s.n.* (UC); Alpine Dam Road, about 1 mi from Alpine Gulch on Fairfax side, 1040', 10 Mar 1968, *Kawahara 29* (CAS); Marin County, 1868-1869, *Kellogg & Harford 713* (CAS); Ross Valley, Apr 1892, *Michener & Bioletti s. n.* (MSC); Tamalpais, Apr 1892, *Michener & Bioletti s. n.* (MSC); Fire road, south side of Mount Tamalpais, 12 Apr 1969, *Mitchell 4* (OSC); Paradise Beach Park, Tiburon Uplands Nature Preserve. N 37°53.329', W 122°26.954', 109', 26 May 1998, *Monfils 18* (MSC); Paradise Beach Park, Tiburon Uplands Nature Preserve. N 37°53.309', W 122°27.055', 137', 3 Apr 1999, *Monfils 34* (MSC); Mt. Tamalpais, 3 Mar. 1930, *Morris s. n.* (RSA); Rcky and clayey bank by Paradise Dr., 0.7 mi. N. Paradise Beach Park, Tiburon Peninsula, 10 Apr 1975, *Norris 2305* (RSA); Tiburon Peninsula, 200', 15 Mar 1930, *Parks 402* (POM, UC); Tiburon, Spring 1926, *Parks* (UC); Alpine Dam Road above Fairfax, 800', 9 Mar 1963, *Sharsmith 5194* (UC); Corte Madera, 1 Mar 1903, *Sheldon 11563* (ORE); Phoenix Lake, Ross, 1000', 4 Apr 1956, *Sprague 1096* (RSA); Carson Ridge, 4 Apr 1957, *Sprague 1120* (RSA); Fairfax, Mar 1928, *Sutcliffe s. n.* (RSA); North slope of hill near Forest Knolls, 21 Mar 1936, *True s. n.* (RSA); Phoenix Lake, Ross, 1000', no date, *no collector* (RSA); Mt. Tamalpais, Apr 1898, *no collector* (CAS). Mendocino County: Abt. 12 mi. e. of U.S. 101, along Calif. 20. In shade above road, 6 Apr 1954, *Clarkson 300* (OSC); Red Mnt., n. Mendocino Co., 21 Jun 1937, *Eastwood & Howell 4663* (CAS); Near Woodville, May 1889, *Howell s. n.* (UC); Ukiah, 25 Apr 1924, *Jones s. n.* (DS-2, POM); Kaiser District, Mar 1903, *McMurphy 306* (DS); 8 mi north of Ukiah, 6 Apr 1938, *Meyer 1384* (UC); Round Valley Historical Marker. N 39°43.749', W 123°15.112', 2160', 25 May 1998, *Monfils 16* (MSC); Round Valley Historical Marker. N 39°43.760', W 123°15.093', 1966', 29 Mar 1999, *Monfils 32* (MSC); Mad River, 6 Jul 1890, *Price s. n.* (UC); Potter Valley, Apr 1894, *Purpus 1009* (UC); Shady Hills, n. Potter Vall., Mar 1894, *Purpus 3089* (UC); Along rte. 128 at MP24.26, 400', 5 Mar 1979, *Smith & Wheeler 5128* (CAS); Red Flat, ¼ mi. from wooden gate btwn, BLM & Coombs property. Red Mnt. N., 2350', 6 Jul 1981, *Smith et al. 6855* (CAS); Summit area of Red Mountain North, 7 Jul 1981, *Smith et al. 6868* (CAS); Seven miles north of Laytonville near highway 101, 20 Apr 1968, *Thomas 14331* (DS); Rte. 253. South of Robinson Creek Rd., Ukiah, 650', 11 Mar 1978, *Wheeler 60* (CAS); South of Leggett on the Old Redwood Hwy, 1000', 1 Feb 1980, *Wheeler 1298* (CAS); Round Valley Historical Marker, overlooking Covelo on Hwy. 162, 2000', 12 Apr 1979, *Wheeler & Smith 905* (CAS); Little River - Albion Road. Near Little River Airport, 600', 23 May 1979, *Wheeler & Smith 1026* (CAS); On Northwesterly slope, 4 mi east of Laytonville, along road to Dos Rios, 20 Mar 1948, *Wiggins 11587* (DS, RSA). Monterey County: Gravel Pitt Hill, 27 Jun 1905, *Dudley s. n.* (DS); Monterey, 1874, *Abbott s. n.* (CAS-2); Carmel Highlands, Peter Pan Rd., 200', 21 Feb 1948, *Balls 7834* (RSA); Monterey, 29 Mar 1933, *Detling 1108* (ORE); Pine Cañon, 1500', 27 Mar 1920, *Duncan 86* (DS); Near Cypress Pt., 28 May 1912, *Eastwood 94a* (CAS); Pacific Grove, 8 Mar 1923, *Eastwood 2471* (CAS); Monterey, 9

Mar 1913, *Eastwood 2489* (CAS); Pacific Grove, Apr 1902, *Elmer 3543* (DS-2, POM, UC); Two miles south of Jolon on hilltop, 10 Mar 1952, *Evans s. n.* (CAS); Sand Stone Cliffs near north fork of San Antonio River, 1500', 27 Mar 1920, *Ferris 1810* (DS); Landels-Hill Big Creek Reserve, Gamboa Point Section, Santa Lucia Mountains, sect. 4, 2 Apr 1982, *Genetti & Engles 48* (CAS); Del Monte Forest, Pacific Grove, 1 Apr 1955, *Howitt 132* (CAS); Pacific Grove, 12 Apr 1933, *Jussel s. n.* (DS); Summit of Hesperia Mountain, north of Bryson, southern Monterey County, 1550', 2 May 1933, *Keck 2093* (DS-2); Near the school, Francis Simes Hastings Natural History Reservation, Santa Lucia Mts., 2 Apr 1944, *Linsdale 71* (CAS); Santa Lucia Mountains, Apr 1898, *Plaskett 75* (UC) Carmel-by-the-Sea, 3 Mar 1910, *Randell 53* (DS); By trail from Carmel to Monterey, 30 Dec 1909, *Randall s. n.* (DS); Parkfield Road, 1.5 mi east of Vineyard Canyon Summit, 2200', 4 Apr 1956, *Twisselmann 2618* (CAS-2); Del Mouh ur. Salinas Road, 15 Apr 1912, *Woodcock s. n.* (POM). Napa County: Mt. St. Helena Trail, 4 May 1928, *Abrams 12265* (DS); Summit of St. Helena Grade, 3 May 1928, *Abrams s. n.* (DS); Howell Mt., 22 Mar 1936, *Cantelow 1142* (CAS); East slope in the Howell Mountains, 5 mi east of Napa, North Coast Range, 1500', 27 Mar 1938, *Constance 2036* (DS, UC); Northern exposure above Putah Creek, along State Hwy. 128, about 6 mi east of Monticello, 26 Feb 1953, *Crampton 989* (UC); 7.2 mi from St. Helena on road to Pope Valley, 2 Apr 1950, *Finrock 17* (UC); Wooded slope in the oak belt about 5 mi south of Calistoga, 12 Apr 1924, *Heller 13840* (DS, POM); Near the summit of the ridges east of Napa on the Monticello road on a clay bank among shrubs, 12 Mar 1940, *Heller 15514* (DS); Wooden Valley road, east side of Napa Range, 8 mi from Napa, 2 Apr 1931, *Keck 1030* (DS, POM); Calistoga, 13 Apr 1929, *Linsdale 257* (UC); Old Howell Mountain Road, 1500', 31 Mar 1967, *Muth 596* (RSA); 1 mi from Pacific Union College, beside road to Pope Valley, 1 May 1949, *Popenoe 18* (OSC); Hills just n. of White Sulphur Ck., w. of Saint Helena, 500', 22 Feb 1954, *Raven s. n.* (CAS); Base of Mt. St. Helena, 3 May 1928, *Wolf 1845* (DS); Summit of Mt. St. Helena Grade, north of Calistoga, *Wolf 1845* (RSA); Upper slopes of Mt. St. Helena, 4 May 1928, *Wolf 1856* (RSA). Nevada County: American Ranch Hills, 5 mi south-west of Grass Valley, on McCourtney Rd., 2200', 8 Apr 1962, *True 356* (CAS). Orange County: 14.3 mi east of San Jaun Capistrano on State 74, 1100', 9 Mar 1962, *Breedlove 1789* (DS); Santa Ana Mountains, Cleveland Nat. Forest. Pleasants Peak (on Orange-Riverside Co. line), 4000', 18 May 1977, *Davidson 5601* (RSA); Sitton Peak Truck Trail: 0.3 mi W of ranger station near hot springs, on Ortega H'way (SR 74), 25 Apr 1990, *Jaroslow B36* (RSA); Sierra Peak Trail, Santa Ana Mts, 11 Apr 1929, *Johnson 1259* (RSA); 5 mi east of Trabuco Oaks, Trabuco Canyon, Cleveland National Forest, 1300', 6 Apr 1966, *Lathrop 6142* (RSA). Riverside County: Santa Ana Mountains, 3 mi above De Luz on dirt road, 3000', 30 Apr 1966, *Adams s. n.* (RSA); Vail Lake area, summit of "Big" Oak Mtn, N. of lake. T7S, R1W, SW $\frac{1}{4}$ sect. 34. Saddle between summits, N slope along rd heading N to Black Hills, 2600', 30 Mar 1990, *Boyd, Ross & Arnseth 3944* (RSA); Vail Lake area, saddle at N base of "Big" Oak Mtn, S of Black Hills. T7S, R1W NE $\frac{1}{4}$, SW $\frac{1}{4}$ sect. 34, 2400', 30 Mar 1990, *Boyd, Ross & Arnseth 3953* (RSA); Santa Ana Mountains, San Mateo Cyn. Wilderness Area.

Tenaja Trail from jtn. W/ Morgan Tr. S to Pigeon Spring area. T6S, R5W sect. 32; T7S, R5W sect. 5, 2200-2600', 31 Mar 1992, *Boyd, Ross & Arnseth 6763* (RSA); Aguata, So. Calif., 7 Apr 1929, *Clark 2035* (RSA); Corona Skyline Drive, Santa Ana Mts. So. Calif., 7 Apr 1929, *Crow 304* (RSA); Vicinity of Beaumont, 17 Apr 1897, *Hall 476* (UC); Aguanga, 22 Dec 1925, *Jaeger s. n.* (POM); Corona, sect. 22, T4S, R7W, 2800', Mar 1934, *Jensen 318* (UC); 18 mi S. W. of Elsinore. South slope of Tenaja Canyon, 2 Apr 1959, *Lathrop 4408* (RSA); 4 mi west of Corona between Tin Mine Canyon & Santiago Peak, Skyline Drive, 4000', 9 Apr 1969, *Lathrop 6968* (RSA); Beaumont, 2000', 25 Mar 1919, *Munz, Street & Williams 2327* (DS, POM); 4 mi. SE of Oak Flat near west county line on Santiago Pk. Fire road near top of peak west of Santiago Pk., Santa Ana Mts., 4200'. 14 Apr 1959, *Ohmsted 374* (RSA); Along roadside in red clay soil, about 4 mi west of Beaumont, on road to Redlands, 19 Mar 1921, *Peirson 2741* (RSA); Rancho Calif. area, ca. 8 mi. (airline) NW of Temecula, between Bruce Lane & Via View Dr. (T 7S, R 1W SBBM NW $\frac{1}{4}$ of SW $\frac{1}{4}$, sect. 27), 2400', 22 Feb 1988, *Pendelton s. n.* (RSA); Santa Ana Canyon, Santa Ana Mountains, 15 Apr 1922, *Pierce s. n.* (POM); 1 mi south of Aguanga, Hwy 79, Agua Tibia Mts., 1940', 12 Apr 1951, *Rush 169* (POM-2); In herbosis, Lambs Canyon proper, Banning, 2300', 25 Apr 1922, *Spencer 1910* (RSA). San Benito County: Eastern exposure on Peak Trail, Pinnacles National Monument, Paicines, 1500', 22 Mar 1955, *Burgess 84* (UC); Pinnacles Nat. Mon., 550 m. 6 Jun 1931, *Fosberg 35251* (RSA); North slope, the Pinnacles, 29 Mar 1930, *Howell 4611* (CAS); Pinnacles National Monument, High Peaks Trail. N 37°53.386', W 122°26.991', 107', 27 May 1998, *Monfils 20* (MSC); Pinnacles National Monument, 1600-1700', 11 May 1940, *Pennell & Powell 25370* (UC); Pinnacles National Monument. Pinnacles Loop Trail, 1200-2500', 27 April 1975, *Thomas 17828* (DS). San Bernardino County: Devore near San Bernardino, 1900', 12 Mar 1928, *Feudge 1960* (POM); Foothills San Bernardino Mts., Apr 1882, *Parish 707* (DS, ORE, UC). San Diego County: Santa Ana Mtns, San Mateo Wilderness Area, "Miller Canyon" on the south base and flank of Miller Mtn from 8S02 upstream to the eastern summit area. T8S,R5W, sect. 10.15, 2100-2900', 3 Mar 1992, *Boyd & Ross 6717* (RSA); W. of Warner Hot Springs, 6 Apr 1929, *Clark 2007* (RSA); South side of Gonzales Canyon, east of Del Mar, 30 Mar 1969, *Copp 69-1* (CAS); Mt. Soledad, 3 Jan 1935, *Gander 103* (RSA, UC); North side of San Miguel Mountain. 32°42'N 116°55'3/4'W, 900', 24 April 1957, *Moran 6000* (DS); Beaumont, 2000', 25 Mar 1919, *Munz, Street & Williams 2327* (ORE); Colorado Desert, 1500', 9 Apr 1921, *Spencer 231* (POM); Potrero Grade, 18 Mar 1917, *Spencer s.n., 9 Apr. 1921* (POM); Grape Vine Canyon, 1200 m, 21 May 1930, *Templeton 1625* (RSA-2); Near Santee, Feb 1915, *Valentien s.n.* (UC). San Luis Obispo County: Atascadero, 22 Mar 1926, *Abrams 10942* (DS); 4.4 mi east of Santa Margarita; La Panza Range, 1200', 29 Mar 1962, *Breedlove 2029* (DS); 3 mi E. of Pozo, sect. 13, T.30S, R.15E. 1800', 27 Mar 1937, *Gifford 801* (UC); 1 mi S. of Bee Rock, Bradley, Sec 7, T.25S, R.10E, 1200', 11 Apr 1938, *Graham 305* (UC); 7X Ranch, Santa Lucia Mountains, 2200', 2 Mar 1956, 2200', *Hardman 143* (CAS); 7X Ranch, Santa Lucia Mountains, 2200', 2 Mar 1956, 2200', *Hardman 144* (CAS); Santa Rita Canyon, Santa Lucia Mountains, 13 Apr 1956, *Hardman 404* (CAS); L. Delagenna

- Ranch, Santa Lucia Mountains, 26 Apr 1956, *Hardman 533* (CAS); Calf Canyon, 5 Apr 1967, *Hoover 10334* (CAS); E. side of Santa Margarita Lake, 8 Apr 1986, *Keil 19136* (RSA); 3 mi N. E. of Templeton, Paso Robles, T. 27S, R. 12E, 900', 31 Mar 1937, *Lee 806* (UC); Growing in a disturbed area on a road bank beside Hwy. #229, 5.9 mi. sw. of Hwy. #41 at Creston, 29 Mar 1981, *McNeal 2433* (OSC); Riconda Trail Head off Pozo Road. N 35°17.214', W 120°28.659', 2200', 18 May 1998, *Monfils 2* (MSC); Riconda Trail Head off Pozo Road. N 35°17.267', W 120°28.677', 2070', 27 May 1998, *Monfils 20*, (MSC); Santa Rita Canyon, 1000', 17 Apr 1957, *Sprague 1136* (RSA); On Cayucos Rd. to Cambira on Jack Mt. Nick Marquat Ranch, 16 Apr 1957, *Sprague 1137* (RSA); Hill by a spring near San Luis Obispo, May 1889, *Summers 527* (CAS); 2 mi north Cuesta Pass, Santa Lucia Mountains, 2000', 4 Apr 1963, *Toschi 63:97* (CAS); Santa Margarita, Eldorado School, 20 Apr 1933, *Wall s.n.* (CAS-2, RSA); Roadside and hills near Adelaide, W. of Paso Robles, 24 Mar 1932, *Wiggins 5847* (CAS, DS, POM); Prefumo Canyon, *no collector* (DS); San Mateo County: Woodside, 16 Mar 1902, *Abrams 2278* (DS); Kings Mountain Road, Santa Cruz Mountains, 500–700', 1 Mar 1914, *Abrams 5058* (POM); Woodside, 3 Mar 1895, *Applegate 421* (DS); Woods on Coal Mine Ridge, 23 May 1937, *Barry 155* (DS); Hill east of Lake Searsville, North Slope, 2 Mar 1929, *Benson 987* (POM); Woodside, Santa Cruz Mtns, near San Fransquito Cr., 600', 28 Feb 1931, *Benson 2610* (POM); Santa Cruz Mountain Peninsula, Crystal Spring Lake, 28 Apr 1920, *Borthwick 97* (DS); Near the intersection of Canada and Edgewood roads. About 3 mi. westward from Redwood City, 13 May 1974, *Cahill 248* (DS); La Honda Road (from Hwy. 5) to Woodside, 3 mi. from Mt. Home-Portola road, 4 Apr 1956, *Campbell 1* (RSA); Big Basin of Pescadero creek, 9 May 1903, *Copeland 3050* (POM); Santa Cruz Peninsula, near Belmont, no date, *Dudley s.n.* (DS); Woodside, 1903 May, *Elmer 4497* (CAS-2, DS, ORE, OSC, POM, UC); Near Belmont, Mar 1886, *Greene 9* (ORE); San Carlos, Chaparral area north of Malabar Rd. and Melendy Dr. Lat N. 37°29'38", Long. 122°16'41"W, 600–680', 22 Apr 1973, *Hemphill 737* (DS); Woods near Spring Valley Lakes, Santa Cruz Mountain Peninsula, 29 Apr 1920, *Hickborn s.n.* (DS); Los Trancos, 30 Apr 1908, *Lewis s.n.* (RSA); Kings Mt., May 1902, *McMurphy s.n.* (DS); Mt. above Woodside, 9 Mar 1906, *McMurphy s.n.* (DS); Sawyer's Road, near Crystal Springs lake above Burlingame and Millbrae, 15 Apr 1956, *O'Bannon s.n.* (DS); Sawyer Ridge, 17 Apr 1949, *Oberlander 86* (DS); Santa Cruz Peninsula, Kings Mt., 27 Apr 1907, *Patterson s.n.* (RSA); Santa Cruz Peninsula, Kings Mt. Road, 27 Apr 1907, *Randall 394* (DS); Santa Cruz Peninsula, Kings Mt. Road, 28 Mar 1908, *Randall s.n.* (DS, RSA); Belmont, 24 Feb 1935, *Rose 35016* (RSA); Crystal Springs lake, 500', 12 Apr 1939, *Rose 39061* (RSA, UC); Millbrae Highlands, 300', 31 Mar 1948, *Rose 48031* (RSA); Emerald Lake, w. of Redwood City, 400', 23 Mar 1964, *Rose 64013* (DS, RSA); 2 mi. nw of Woodside, 600', 27 Mar 1969, *Rose 69009* (MSC); King's Mountain, 27 Apr 1907, *Rust 135* (RSA); King's Mountain Road, 29 Mar 1949, *Thomas 195* (DS); Jasper Ridge, about 5 mi southwest of Palo Alto. Lat N. 37°24.5', Long. 122°14' W, 500', 5 Apr 1959, *Thomas 7663* (MSC); ½ way up east slope of La Honda Grade, Santa Cruz Mts., 24 Jan 1927, *Wolf 190* (RSA); East side of La Honda Grade, 26 Feb 1927, *Wolf 221* (RSA); Above Searsville Lake, 2 Mar 1927, *Wolf 235* (RSA). Santa Barbara County: Purissima Hills, on road to Mission, 27 Mar 1938, *Abrams 13755*, (DS); North side of the Point Sal Ridge, 3 ½ mi. west of Corralillos Canyon. Point Sal, 3 Mar 1958, *Blakley & Muller B-2695* (CAS-2, RSA); Beside Refugio Pass Road, 5.4 mi north of U.S. 101, 24 Feb 1962, *Breedlove 1778* (DS); San Marcos Pass. Old Stagecoach Road. N 34°31.790', W 119°50.070', 1402', 17 May 1998, *Monfils 1* (MSC); Old Freemont Trail and Coach Rd., Santa Ynez Mts., Area of Refugio Pass, 2200', 18 Mar 1956, *Pollard s.n.* (CAS); Near summit of Refugio Pass, Santa Ynez Mts, 2200', 19 Apr 1968, *Pollard s.n.* (CAS); Stagecoach Road, 1650', 5 Apr 1970, *Shevock 106* (RSA); Entrance to Foster Glen Park, along highway in San Marcos Pass, south side of Santa Ynez Mountains near summit, 11 Mar 1955, *Smith 3918* (RSA, UC); Three miles north of summit of San Marcos Pass, 19 Mar 1961, *Turner, Sphon & Ball C-494* (RSA). Santa Clara County: Santa Cruz Peninsula, charcoal burners, Page Mill Road, Black Mt., 6 Jul 1903, *Dudley s.n.* (DS); Santa Cruz Peninsula, Page Mill Road, Black Mt., 23 Apr 1904, *Dudley s.n.* (DS); Adelante Villa, Palo Alto, 25 Feb 1894, *A. M. K. s.n.* (RSA); Foothills near Stanford University, 9 Mar and 15 May 1902, *Baker 283* (CAS, DS, MSC-2, POM, UC); Black Mt., 9 Feb 1895, *Burnham 9 Feb. 1895* (MSC); Eastern slope of Mount Hamilton, 3000', 31 Mar 1933, *Chambers 144* (UC); Los Gatos, 19 Mar 1897, *Davy s.n.* (UC); North-facing bank, south side of page Mill road, ca. 1 mi west of entrance to Palo Alto Foothills Park, Palo Alto, 1200', 25 Mar 1969, *Doty 593* (RSA); Foothills west of Los Gatos, 25 Mar 1904, *Heller 7281* (DS, MSC, UC); Alpine Creek Road, northeast side of Santa Cruz Mountains, 200', 22 Feb 1932, *Keck 1387* (DS, RSA); Foothills of the eastern side of the Santa Cruz Mountains, 5 mi south of the center of Palo Alto. Los Tracos Trail above Los Tracos Creek, 600–1800', 3 Apr 1974, *Martineau 16* (DS); 23.1 mi. w. of Interstate #5, Patterson exit, in Del Puerto canyon (2.5 mi. e. of the Mt. Hamilton-Livermore Rd.), 15 Mar 1970, *McNeal 472* (OSC); Fire trail near Loma base above spring, 3400', 21 Mar 1940, *Nelson 71* (UC); Hills 1 ½ miles south of Saratoga, Western Santa Clara County, 800', 1 Mar 1906, *Pendleton 290* (POM); 10 mi south of Black Mountain, s. of Palo Alto, 1200–1300', 16 May 1940, *Pennell & Abrams 25429* (CAS, UC); Seeby Ridge, Mount Hamilton Range, 2400', 10 Feb 1934, *Sharsmith 537* (UC); South end of Mount Day Ridge above Santa Isabella Creek, Mount Hamilton Range, 1800', 25 Mar 1935, *Sharsmith 1520* (UC); Northwest slope of Black Mountain, 1100', 31 Jan 1948, *Silva 2616* (RSA); Vicinity of Mt. Umunhum, Lat. N. 37°09.5', Long. 121°54.2' W, 3400', 23 Apr 1954, *Thomas 3963* (DS). Santa Cruz County: Ben Lomond Mountain area; on Eagle Rock; T9S, R3W, sect. 16, 2200', 23 Mar 1974, *Halse 986* (OSC); Big Basin, Santa Cruz Mts., *Reed s.n.* (CAS); Santa Cruz Peninsula, Swanton, Spring 1912, *Rich s.n.* (DS); La Honda Rd. Sta. Cruz Mts., 2000', 3 Apr 1956, *Sprague 1095* (RSA); Between Eagle Rock and Locatelli Ranch. Lat. N. 37°08.7', Long. 122°12'W, 2400', 27 Mar 1950, *Thomas 1346* (DS); East side of Mill Creek Drainage about 2 mi S-SW of Eagle Rock at Lat. N. 37°07.3', Long. 122°12.4'W, 1800–1900', 30 Apr 1954, *Thomas 3035* (DS); Between Eagle Rock and Locatelli Ranch. Lat. N. 37°08.7', Long. 122°12'W, 2200', 15 Mar 1954, *Thomas 3776* (DS); Vicinity of Eagle Rock. Lat N. 37

08.8. Long. 122 11.7 W. 2200–2500', 30 Mar 1961, *Thomas 9041* (DS); Halfway down La Honda Rd. Sta. Cruz Mts., 2000', 13 Apr 1957, *no collector* (RSA); Solano County: Gates Canyon, northwest of Vacaville, 3 Mar 1951, *Kehler s. n.* (OSC); 3 ½ miles west of Rockville, 25 Mar 1966, *Olson & Gorelick* (RSA-2). Sonoma County: Pepperwood Ranch, Oak woodland between the 2 fir-Redwood canyons, 25 Mar 1981, *Denevers 565* (CAS); Calistoga, 25 Mar 1922, *Eastwood 11097* (CAS); Camp Meeker, 22 Mar 1924, *Howell 287* (CAS); Near Sonoma, Mar 1962, *Menzins s.n.* (CAS); 2 mi from juncture of Highway 12 and Trinita Road, 750', 27 Feb 1960, *Ruckert 5* (CAS). Sonoma County, 10 Mar 1903, *Rattan s.n.* (DS); 0.5 mi. south of Calistoga, 400', 29 Mar 1953, *Raven 5207* (CAS); Santa Rosa Creek Canyon, 8–10 mi east of Santa Rosa, 25 Mar 1937, *Robbins 10* (UC); N. side of Vine Hill School Road ½ miles from Vine Hill Road, 250', 19 Apr 1965, *Thorne 34319* (RSA); Parker Hill Rd. ca. 2 ½ mi. N of Santa Rosa and 1 mi. N of Sonoma Co. Hosp., 350', 20 Apr 1965, *Thorne 34328* (RSA). Stanislaus County: Near head of Del Puerto Canyon, 20 Apr 1941, *Hoover 4886* (UC). Trinity County: Vic. Dam at Ruth Reservoir on Mad River, 2700', 21 May 1979, *Mattoon 121* (RSA, UC); Road along Coffee Creek, above Coffee Creek Ranch, 16 Jun 1956, *McClintock s. n.* (CAS); T6N, R6E, sect. 34, Found in Grays Falls Campground, 21 Apr 1979, *Miller 2-87* (RSA); sect. 10, T4S, R7E, West slope of Salt Cr., 2400', 28 May 1933, *Sack & Iverson*

70393 (CAS); New River Trail from Grays Falls Campground on the North side of the Trinity River and west side of the New River, 800–1000', 7 Apr 1973, *Smith 6006* (RSA); Under scattered yellow pine; along Van Duzen River, about 3 mi southeast of Kuntz, 20 Apr 1950, *Tracy 18633* (RSA, UC). Ventura County: Las Turas Lake, Santa Monica Mts., 14 Feb 1931, *Ewan 4027* (POM); Upper Ojai, Ojai Valley and vicinity, 7 Mar 1895, *Pettibone & Hubby s.n.* (CAS); Hills north of Ojai, Upper Ojai, Ventura River Basin, 16 Apr 1949, *Pollard s. n.* (CAS); Hills north of Ojai, Upper Ojai, Ventura River Basin, 21 Apr 1949, *Pollard s. n.* (CAS), County Unknown: Belmont (MSC); California, 1853–1854, *Bigelow s.n.* (DS); S. Oakland Hills, Mar 1900, *Carruth s.n.* (CAS); Mt. Hamilton, 3000', 3 Apr 1906, *Chauler 6014* (UC); Cuesta Summit, 2600', 2 Apr 1908, *Condit s.n.* (UC); California, *Coulter s.n.* (UC); Mt. St. Helena, 1 May 1918, *Eastwood 6811* (CAS, UC); Near Woodville, May 1889, *Howell 1387* (ORE); Northern California, 7 Apr 1937, *Javete s.n.* (OSC); Napa River Basin, Trail to beaux's Cabin, 25 Apr 1893, *Jepson s.n.* (UC); Near San Jaun Hot Springs, 6 Mar 1913, *Perkins s.n.* (RSA); Oakland, 1903, *Rattan s.n.* (DS); California, 1889, *Wright s.n.* (UC). MEXICO: **Baja California:** Elev. Of peak with microwave towers at 1275 m, 32°19'N–116°40'W, collections made from peak to base (ca. 600 m), *Thorne et al. 62130* (CAS, RSA).